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Jointed Goatgrass (*Aegilops cylindrica*) by Imidazolinone-Resistant Wheat Hybridization under Field Conditions

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Gene flow between jointed goatgrass and winter wheat is a concern because transfer of herbicide-resistance genes from imidazolinone-resistant (IR) winter wheat cultivars to jointed goatgrass could restrict weed-management options for this serious weed of winter wheat cropping systems. The objectives of this study were (1) to investigate the frequency of interspecific hybridization between IR wheat and jointed goatgrass in eastern Colorado, and (2) to determine the gene action of the IR acetolactate synthase (ALS) allele in IR wheat by jointed goatgrass and in IR wheat by imidazolinone-susceptible (IS) wheat backgrounds. Jointed goatgrass was sampled side-by-side with IR wheat and at distances up to 53 m away in both experimental plots and at commercial field study sites in 2003, 2004, and 2005. A greenhouse-screening method was used to identify IR hybrids in collected jointed goatgrass seed. The average percentage of hybridization across sites and years when IR wheat and jointed goatgrass were grown side-by-side was 0.1%, and the maximum was 1.6%. The greatest distance over which hybridization was documented was 16 m. The IR ALS allele contributed 25% of untreated ALS activity in jointed goatgrass by IR wheat F_1 plants, as measured by an in vitro ALS assay. The hybridization rate between wheat and jointed goatgrass and the expression of the IR wheat ALS allele in hybrid plants will both influence trait introgression into jointed goatgrass.

Nomenclature: Jointed goatgrass, *Aegilops cylindrica* Host AEGCY; hard red winter wheat, *Triticum aestivum* L. 'Above', 'Bond', 'Prairie Red', 'Halt'.

Key words: Herbicide-resistant crops, hybridization, pollen-mediated gene flow.

Gene flow between crops and related weeds is a concern because crop genes may improve weed fitness or restrict weed management options. A reliable estimate of crop–weed hybridization rates under natural conditions is required to determine potential fitness consequences of transferring crop herbicide-resistance traits (Hails and Morley 2005). Novel single-gene traits conferring identifiable phenotypes may now be used to evaluate current hybridization rates; however, introgression must occur for crop traits to affect weed fitness. Introgression is defined as the transfer of genetic material between species through hybridization and several generations of backcrossing (Hegde and Waines 2004). Gene flow and selection may work together to increase introgression rates (Ellstrand et al. 1999).

Jointed goatgrass is a serious weed in winter wheat cropping systems in the western United States (Donald and Ogg 1991). Jointed goatgrass, a tetraploid with 28 chromosomes, shares the D genome from Tausch's goatgrass (*Aegilops tauschii* Coss.) with bread wheat, a hexaploid with 42 chromosomes (Kimber and Sears 1987). Although the two species are predominantly self-fertilizing, cross-pollination can result in a partially fertile hybrid, and restoration of tetraploid or hexaploid chromosome number is possible with repeated backcrossing to jointed goatgrass or wheat, respectively (Schoenenberger et al. 2005; Snyder et al. 2000; Wang et al. 2001; Zemetra et al. 1998).

Wheat cultivars resistant to the imidazolinone-herbicide imazamox have been developed through induced mutagenesis followed by conventional plant breeding (Baenziger et al. 2006; Berg et al. 2006; Haley et al. 2003, 2006a, 2006b; Lazar et al. 2003; Newhouse et al. 1992; Souza et al. 2006). These cultivars allow selective control of jointed goatgrass and other winter annual grass weeds with imazamox during the growing season (Geier et al. 2004). Imidazolinone herbicides inhibit acetolactate synthase (ALS; EC 4.1.3.18), an enzyme involved in the synthesis of branched chain amino acids (Shaner et al. 1984), and ALS in imidazolinone-resistant (IR) wheat cultivars is not sensitive to these herbicides (Tan et al. 2005). The introduction of IR wheat cultivars creates an opportunity for crop–weed hybrids to have a selective advantage and increase the probability of gene transfer from wheat to jointed goatgrass, making the herbicide weed-control option potentially ineffective.

Wheat contains three homoeologous ALS genes (Pozniak et al. 2004), which have been characterized as partially dominant in several spring wheat lines (Pozniak and Hucl 2004). An in vivo ALS activity assay demonstrated that wheat lines heterozygous for the ALS-resistance trait were distinguishable from homozygous wheat lines because the imazamox dose required to inhibit ALS activity of heterozygous wheat was 69 to 81% less than the dose required for homozygous wheat (Rainbolt et al. 2005). The gene action of the imidazolinone resistance trait is relevant to the hybridization and introgression rates between IR wheat and jointed goatgrass. First-generation hybrids will be heterozygous for the IR trait, and the gene action of herbicide resistance influences the rate at which the resistance allele will increase in frequency in a population under selection (Jasieniuk et al. 1996).

Protein and morphological markers have been used to monitor the frequency of hybridization between wheat and jointed goatgrass (Kroiss et al. 2004; Stone and Peeper 2004). Herbicide resistance provides another identifiable marker useful for screening large samples and is relevant to the gene introgression issue (Hanson et al. 2005). The frequency at which hybrids occur has been evaluated in the Pacific Northwest by Hanson et al. (2005) and Morrison et al. (2002b); in Oklahoma, by Stone and Peeper (2004); and in Europe, by Guadagnuolo et al. (2001). Hybrids are known to

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occur in eastern Colorado, but no information is available on the hybridization frequency in this region. Increasing use of no-till systems and the rapid adoption of IR wheat technology in eastern Colorado have created a unique environment in which selection intensity and potential fitness advantages for jointed goatgrass could be significant. The objectives of this study were (1) to investigate the frequency of interspecific hybrids between wheat and jointed goatgrass using imidazolinone resistance as a marker, and (2) to establish the gene action of the herbicide-resistance ALS allele in a jointed goatgrass by resistant-wheat cross and in a susceptible-wheat by resistant-wheat cross.

Materials and Methods

Plot Locations and Design. Both commercial field sites and experimental plots were used to detect hybridization between IR wheat and jointed goatgrass. Commercial field sites were located in eastern Colorado by scouting and identifying commercial IR winter wheat fields in which jointed goatgrass was growing or was in close proximity to IR winter wheat during the summers of 2003, 2004, and 2005. The IR winter wheat cultivars included 'Above' (Haley et al. 2003) and 'Bond CL' (Haley et al. 2006).

The experimental plots were planted in the fall of 2003 and 2004. All planted jointed goatgrass seed was collected from a wheat seed-cleaning facility in northeastern Colorado. A Nelder wheel design (Nelder 1962) was planted with a conventional six-row cone seeder in the fall of 2003 at the U.S. Department of Agriculture (USDA), Central Great Plains Research Station, in Akron, CO. The experiment had a central 10 by 10 m block of Above winter wheat and eight rays of jointed goatgrass that were 1.1 m wide and 45 to 53 m long emanating from the center. Two IS winter wheat cultivars 'Prairie Red' (Quick et al. 2001) and 'Halt' (Quick et al. 1996) were planted in alternating 1.1-m-wide strips surrounding the center Above block. These cultivars were included to simulate IS wheat pollen competition. The experiment was designed to place jointed goatgrass within and at multiple distances and directions away from IR wheat. Wind speed and direction were recorded from a permanent USDA weather station located 400 m from the site.

Additional experimental locations were planted with jointed goatgrass in fall 2004. These sites included 10 by 10 m blocks of Above at Akron and Platner, CO, planted with a cone seeder, and 10 by 20 m blocks of Above and Bond CL at Fort Collins, CO, planted with a single-row push-type seeder with disc openers. Heading dates were recorded for each species in all experimental plots to estimate the overlap of flowering periods between wheat and jointed goatgrass.

Sample Collection. All samples were collected by hand-harvesting jointed goatgrass spikes in maturing wheat fields in June or July. In summer 2004, the Nelder wheel was sampled for jointed goatgrass in 1-m^2 plots at distances from 1 to 53 m in eight compass headings from the central block of Above. Samples were also collected from individual jointed goatgrass plants growing within the central Above block. Samples could not be collected from all locations in 2004 because of poor jointed goatgrass emergence. In summer 2005, multiple 1-m^2 jointed goatgrass samples were collected from within the IR wheat blocks at experimental plot locations. Jointed goatgrass was located and sampled at several distances up to 23 m from the Akron, CO, block of Above in 2005.

At commercial field sites jointed goatgrass spikes were sampled and the distance from jointed goatgrass to IR wheat was measured. All samples were placed in labeled bags and processed by hand to remove straw and to break spikes into individual spikelets.

Sample Screening. All jointed goatgrass seed samples were planted in 60 by 30 cm flats filled with potting medium.[1] Fifteen spikelets were planted on 3 cm of potting mix in each of 12 rows and covered with an additional 2 cm of potting mix. A total of 720 spikelets were planted in four flats (two replications of two flats) for each sample, representing from 10 to 100% of total spikelets per sample. Control flats were planted with Above, Prairie Red, and heterozygous IR seed derived from crossing Above and Prairie Red. Seedlings were grown to the two- to three-leaf stage in the greenhouse before spraying with imazamox at 44 g ae ha^{-1} in combination with 0.25% (v/v) nonionic surfactant and 1.0% (v/v) urea ammonium nitrate in a pressured spray chamber calibrated to deliver 187 L ha^{-1} at 206 kPa. Seedlings were clipped to 1 cm above the newest emerging leaf with electric shears 2 d after spraying and plants that regrew were identified as resistant, in comparison to regrowth on heterozygous wheat plants in control flats. The total number of plants that germinated in each flat was recorded along with the number of survivors. All plants surviving herbicide treatment were verified as hybrids either by vernalizing at 2 C for 8 wk to initiate floral development and examining spike morphology, or by mitotic root-tip chromosome counts (Tsuchiya 1971). Somatic chromosome number of 35 (ABCDD, $2n = 5x = 35$) indicated a true hybrid, whereas a count of 28 (CCDD, $2n = 4x = 28$) (Kimber and Sears 1987) indicated that a plant was jointed goatgrass and should not be included in the survivor total. Percentage of hybridization was calculated by dividing the number of confirmed survivors by the number of total plants screened in each sample.

Analysis of Gene Action. To determine the gene action of the mutant ALS allele in a jointed goatgrass background, F_1 hybrids were developed by hand-pollination using jointed goatgrass as the maternal parent and Above as the paternal parent. Heterozygote wheat seed from controlled crosses of IS Prairie Red × IR Above also were developed. An in vitro ALS activity assay was used to quantify resistance to imazamox using a method modified from Hanson et al. (2006). Seeds from the crosses were planted in 30 by 30 cm flats filled with potting mix and grown under greenhouse conditions. Crude protein, including ALS, was extracted from a bulked sample of 30 stems from 30 individuals of Above, Prairie Red, jointed goatgrass, and Prairie Red × Above F_1. Because of a limited seed supply, one individual from each of seven jointed goatgrass × wheat F_1 plants was used for crude protein extraction. Plants were sampled at the three- to five- leaf stage. The ALS assay was performed in 96-well plates by adding 50 μl of crude protein extract to 50 μl of three different reaction solutions. The first reaction solution was a distilled water control, the second was 50 μM of imazamox, and the third was 100 μM of ACC 299,016,[2] which inhibits all forms of ALS enzyme (Alvarado et al. 1992). Each reaction solution

Table 1. Hybridization rates in jointed goatgrass growing side by side with imidazolinone-resistant winter wheat in Colorado during 2004 and 2005.

Year	Site	Samples	Plants Screened	Hybrids	Hybridization
		no.			%
2004	Akron	15	8,432	13	0.15
	Commercial fields	1	753	12	1.60
2005	Fort Collins, 'Above'	10	9,531	1	0.01
	Fort Collins, 'Bond CL'	10	7,277	0	0.00
	Platner	3	2,154	0	0.00
	Akron	18	4,842	11	0.23
	Commercial fields	10	5,783	2	0.03
Total		67	38,772	39	0.10[a]

[a] Mean hybridization (%) of all samples.

was replicated eight times within the experiment. Total acetolactate produced was measured by decarboxylating acetolactate to acetoin and spectrophotometrically measuring absorbance at 535 nm according to the methods of Westerfeld (1945). The background absorbance of the ACC 299,016 treatment was subtracted from the control and imazamox treatment to determine acetolactate production. Final data were expressed as micromoles acetolactate produced per mg protein per hour.

Acetolactate synthase activity in the imazamox treatment, expressed as a percentage of the control, was used in a modified-generation means analysis to calculate the midparent value, additive gene effect (a), and dominance effect (d) in SAS PROC GLM (SAS 2004). The parameter a is calculated as the difference between the two parents divided by two, and d is the difference between the F_1 and the midparent values (Kearsey and Pooni 1996).

Results and Discussion

Hybridization. Dates of 50% heading for IR wheat and jointed goatgrass in experimental plots were 3 d or less apart. Jointed goatgrass samples taken within IR wheat showed substantial variation in hybridization rates among sites and years (Table 1). Variable environmental conditions at different sites likely explain the range of hybridization rates observed in this study. The average percentage of hybridization across sites and years when IR wheat and jointed goatgrass were growing side by side was 0.1% (Table 1). This result is consistent with an average of 0.07% hybrids found by Stone and Peeper (2004) in jointed goatgrass seed from bulk wheat delivery at grain elevators.

Hybridization was observed in three jointed goatgrass samples at 0.3, 1.2, and 16 m from IR wheat in the experimental sites (Table 2) but not in 13 samples collected from 0.3 to 13 m from commercial IR wheat fields (Table 2). Wind speed and direction did not appear to influence hybridization over distance, although the small number of hybridization events at any distance from IR wheat limited the ability to detect relationships with wind speed. The maximum distance over which hybridization was observed was 16 m (Table 2), less than the previously reported maximum of 40.2 m (Hanson et al. 2005). The shorter maximum distance in this study may be because of different environmental conditions in study locations or because the frequency of hybridization at farther distances was lower than could be detected in this experiment.

Previously reported maximum hybridization rates have varied from 0.52% by Hanson et al. (2005) to 8% by Morrison et al. (2002b). The maximum hybridization in any sample from this study was 1.6% (Table 1). This sample site was a commercial wheat field where the farmer planted IR wheat into a field heavily infested with jointed goatgrass and subsequently decided not to spray imazamox because of poor crop condition. The wheat crop did survive to maturity and had a high probability of pollinating plants in the dense jointed goatgrass population. This observation supports proper imazamox application as a component of resistance management plans that are intended to minimize the risk of introgressing imidazolinone resistance into jointed goatgrass (Seefeldt et al. 1998; Tan et al. 2005).

The numbers of sites (16), samples (141), and total plants screened (61,350) to obtain these results represent sufficient sampling to document hybridization between wheat and jointed goatgrass in Colorado. A different wheat production system exists in the central-western Great Plains than in locations where previous studies have been conducted because of the rapid adoption of IR wheat technology and increasing use of no-till practices. Previous studies demonstrated potential for trait introgression from wheat to jointed

Table 2. Hybridization rates in jointed goatgrass growing at various distances from imidazolinone-resistant (IR) winter wheat in CO during 2003, 2004, and 2005.

Year	Site	Distance	Samples	Plants Screened	Hybrids	Hybridization
		m	no.			%
2003	Commercial fields	0.3 to 13	3	2,034	0	0.00
2004	Akron	0.3 to 53	47	10,435	0	0.00
		0.3[a]	1	342	1	0.29
		1.2[b]	1	193	1	0.20
	Commercial fields	0.3 to 1	5	2,629	0	0.00
2005	Akron	0.3 to 22.8	11	4,163	0	0.00
		16[c]	1	173	1	0.60
	Commercial fields	0.3 to 2.2	5	2,609	0	0.00

[a] Sampled northwest of IR wheat.
[b] Sampled east of IR wheat.
[c] Sampled south of IR wheat.

Table 3. Results of a modified-generation means analysis in two crosses for in vitro acetolactate synthase (ALS) activity under inhibition with 50 μM imazamox.[a]

Genetic cross	Parameter[b]	ALS Activity[c]	*d*/*a* ratio	Gene action
		%		
JGG × Above	*m*	30.99**	0.59	PD
	a	15.32**		
	d	9.08*		
Prairie Red × Above	*m*	23.15**	0.10	A
	a	23.15**		
	d	2.43 NS		

[a] Abbreviations: PD, partial dominance; A, additive; NS, not significant.
[b] Parameters: *m*, midparent value; *a*, additive effect; *d*, dominance effect.
[c] Percentage of untreated control ALS activity.
* $P < 0.01$; ** $P < 0.0001$ level

goatgrass when hybrids occur in close proximity to jointed goatgrass, which allowed advanced generation backcrosses to form (Morrison et al. 2002a; Snyder et al. 2000), with most F_1 hybrids having jointed goatgrass as the female parent and most first-generation backcross plants having wheat as the male parent (Gandhi et al. 2006). Hybrids between IR wheat and jointed goatgrass in our study indicate the potential for movement of imidazolinone resistance or other single-gene traits from wheat to jointed goatgrass in the central-western Great Plains region.

Gene Action. The ratio of dominance to additive effects indicates gene action when determined by a quantitative measurement such as in vitro ALS activity. According to Stuber et al. (1987), a *d*/*a* ratio, less than 0.2 indicates additive gene action, 0.2 to 0.8 indicates partial dominance, 0.8 to 1.2 indicates dominance, and greater than 1.2 indicates overdominance. Data from the in vitro ALS-activity assay indicated that the mutant D genome ALS allele from Above was expressed in jointed goatgrass × Above F_1 plants and that the resistance allele was partially dominant in a jointed goatgrass × Above cross (Table 3). Both *a* and *d* were significant ($P < 0.01$), and the *d*/*a* ratio was 0.59 (Table 3). In a Prairie Red × Above cross, the resistance allele was additive with no significant dominance effect, and the *d*/*a* ratio was 0.1 (Table 3). These results demonstrate that jointed goatgrass × IR wheat F_1 hybrids have physiological expression of the resistant-ALS enzyme, which is consistent with observed whole-plant resistance following imazamox treatment. Under imazamox treatment, the IR D genome ALS allele from Above contributed approximately 25% of untreated ALS activity in both crosses. Therefore, the statistical difference in gene action may be due to moving the resistance gene between species of different ploidy levels and not because of a biological difference in gene action of the D genome resistance allele.

Each homoeologous genome of bread wheat contains one locus encoding ALS, with the D genome contributing the greatest catalytic activity (Pozniak et al. 2004). When the in vitro imazamox treatment completely inhibits ALS activity in a susceptible wheat line (Figure 1), it is assumed that all sensitive forms of the enzyme in resistant cultivars are also inhibited (Hanson et al. 2006). The mutant D genome allele from Above presumably represents one out of five translated ALS alleles in the jointed goatgrass × Above background ($2n = 5x = ABCD_{Jointed\ goatgrass}D_{Above}$) and one out of six translated ALS alleles in the Prairie Red × Above background ($2n = 6x = AABBD_{Prairie\ Red}D_{Above}$). Figures 1 and 2 demonstrate the effect of additional ALS alleles. Jointed goatgrass had less acetolactate produced per milligram protein than the wheat lines, and the jointed goatgrass × Above F_1 was intermediate (Figure 1). The total ALS activity in the jointed goatgrass × Above F_1 was less than the total ALS activity in the three wheat lines (Figure 1). If the mutant D genome ALS allele is transcribed and translated equally in the jointed goatgrass × Above F_1 and the Prairie Red × Above F_1, the contribution of one functional mutant genome allele under imazamox treatment (Figure 2) should represent a greater proportion of total ALS activity in a jointed goatgrass × IR wheat hybrid than in heterozygous resistant wheat. Therefore, the higher midparent value in the jointed goatgrass × Above background (31%) than in heterozygous wheat (23%) is reasonable.

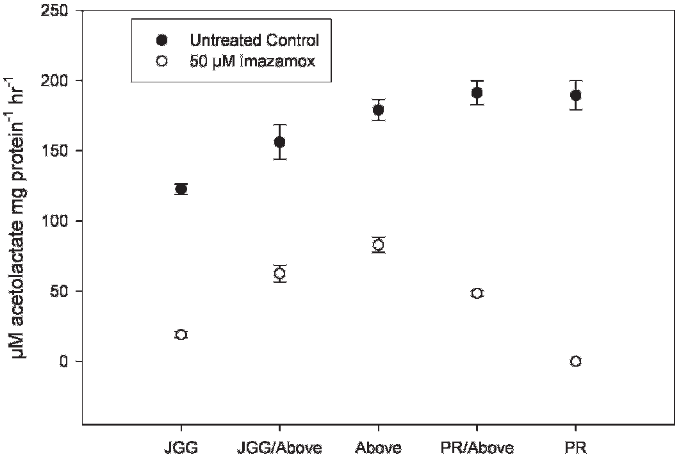

Figure 1. Mean and standard error of in vitro acetolactate synthase (ALS) activity in jointed goatgrass (JGG), Above wheat, Prairie Red (PR) wheat, PR × Above F_1, and JGG × Above F_1 in an untreated control and under inhibition with 50 μM imazamox.

In summary, low-level hybridization between IR wheat and jointed goatgrass was documented under central-western Great Plains field conditions. Hybrids were detected among jointed goatgrass progeny as survivors of imazamox treatment and were further confirmed with evaluation of spike morphology or chromosome number. The average hybridiza-

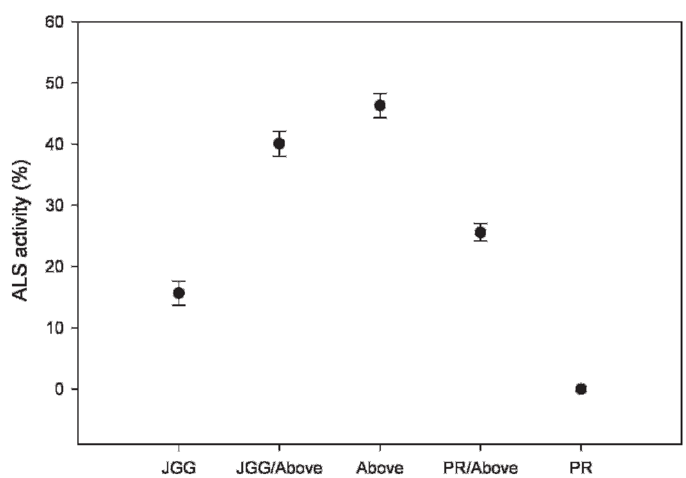

Figure 2. Mean and standard error of in vitro acetolactate synthase (ALS) activity under inhibition with 50 μM imazamox expressed as percentage of untreated ALS activity in jointed goatgrass (JGG), Above wheat, Prairie Red (PR) wheat, PR × Above F_1, and JGG × Above F_1.

tion rate was 0.1% and the maximum distance over which hybridization occurred was 16 m. Expression of the resistant ALS allele from IR wheat was confirmed in jointed goatgrass by wheat hybrids and genetic analysis determined that the trait is partially dominant in this background. The hybridization rate between these two species and the partial dominance of the resistance trait will influence the fitness value and introgression rate of the resistance allele in a jointed goatgrass population exposed to imidazolinone herbicide-selection pressure. These data will be useful for future risk assessment of transgenic herbicide-resistant wheat cultivars.

Sources of Materials

[1] Sunshine Mix #3, SunGro Horticulture, 15831 N.E. 8th Street, Suite 100, Bellevue, WA 98008.

[2] BASF Corporation, Research Triangle Park, NC 27709.

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